THE BROWN ARGUS BUTTERFLY IN NORTH-WEST EUROPE

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Introduction

A SUBSTANTIAL paper by Høegh-Guldberg, 1966 (OH-G) on the Brown Argus in Denmark, Norway and Sweden contains details on many aspects of the *Ariciae*. Among these are results of cross-breeding experiments between parents from southern England (*A. agestis*), Durham (*A. salmacis*), north Denmark, southern Norway and Sweden, the three latter all forms of *A. allous* according to OH-G. This work was carried out in collaboration with F.V.L. Jarvis in Britain. In addition to this a great deal of data is presented by OH-G on selected colonies from the above three Scandinavian countries, including lunulation and the occurrence of several varieties.

Lunulation refers here to the series of orange spots near the margins of the upper forewing and hindwing with a maximum of six on each. It is generally accepted that *agestis* is well lunulated while *allous* is poorly lunulated: in previous papers the author (Smyllie, 1992a and 1992b) has shown that by quantifying upper forewing lunulation it is possible to classify British colonies according to the degree of lunulation shown by the whole colony rather than by any one individual in it. The main objective in this paper is the comparison of OH-Gs lunulation data for Scandinavia with my data for Britain, after the figures have been manipulated to allow this. Reasons for any modifications are given followed by the resulting Tables A and B. A discussion section follows involving the data generated, and including descriptions of and comments on four varieties. Broad similarities are shown to exist in both varieties and lunulation patterns between Britain and Scandinavia. Finally the main conclusions are summarised.

Lunulation Tables

In the following tables data is taken or modified from Høegh-Guldberg (1966) and Smyllie (*loc. cit.*). When any English or Scottish counties are mentioned, these have the former boundaries. All the 23 museum collections examined were completed before the present names and boundaries were introduced. The data for the OH-G tables has been originally supplied by Helge Rambring, a Swedish lepidopterist, who recorded the total number of orange lunules on the upper side of each specimen. Initially I did the same but soon dropped the hindwing count as I found that forewing lunulation (upfl) was more varied. Both forewing and hindwing lunulation (uphl) can vary between 0 and 6. Only occasionally do 6 occur on the uph. The norm for 5 and 6 upfl males is 5 uphl. Prints of 22 males with 5 upfl from English *agestis* and *salmacis* colonies were examined and all had 5 uphl. Females are better lunulated than males, and for a 6 upfl female I have not seen less than 5 uphl. In order to compare lunulation figures, males and females had first to be classified as well lunulated (C) or poorly lunulated (P) from the Jarvis terms *crassilunulata* and *parvilunulata* respectively (Jarvis, 1966). C males were required to have 5 or 6 upfl while C females (which are better lunuated) needed 6, traces or more counting as a full lunule. It follows that P males have 0–4, females 0–5 upfl. In converting the OH-G Tables I have counted males with 10, 11 or 12 lunules as C, 0–9 as P, while females with 11 or 12 are C and 0–10 are P. The resulting Table A summarises males (M) from any colony/area as MC or MP where MC+MP=MT (T=total). Similarly for females FC+FP=FT. These figures are combined on a 50/50 basis by reducing the larger proportionally so that MT=FT, and adding up to give combined figures CC and CP where CC+CP=CT=2MT or 2FT.

All figures for any site are amalgamated to compare with my data, and the right-hand column gives the CC:CP ratio, a numerical figure which expresses the degree of lunulation – the higher the figure the better the lunulation and vice-versa. A much more complete Table of British sites is given in Smyllie (*loc. cit.*).

OH-G has split upfl and uphl into four categories:

I combinations of 4-6 upfl and 4-6 uphl

II – IV 0-3 upfl with combinations of uphl.

Because of the complication of uphl the comparison has to be restricted to 6, 5 and 4 upfl (category I). This can be matched by selected data from Smyllie (*loc. cit.*) which gives complete numerical details for male upfl for several British sites, plus similar information on females from the general data bank. Over a wide range of variation it is felt that a combination of both sexes gives a more complete picture. Table B gives 4-6 upfl expressed as a percentage of the total number checked. The numbers from which percentages have been derived are included. The higher the numbers the more stable the figures. Although more tentative, low figures (say <15) are better than nothing and do give some indication, so have been included.

Discussion

Lunulation

Conclusions from the Smyllie papers have to be stated as a necessary preliminary to any comparison of data. The three relevant sub-species of *Ariciae* involved are set out and described. I call them sub-species because they are capable of interbreeding – no other reason. They are referred to by their specific names for simplicity, and as far as I am aware there are no other species in Europe capable of interbreeding:–

1. *agestis*. Well lunulated with a dark upf discal spot.
2. *artaxerxes*. Poorly lunulated with a white upf discal spot.
3. *allous*. Poorly lunulated with a dark upf discal spot.

1. In England *agestis* occurs from the south coast up to and including three univoltine areas, Eyarth Rocks, the Peak District and the Yorkshire Wolds.

All these populations have CC:CP ratios >5.0 (Table A), and this figure gives a rugged and stable quantified measure of *agestis* lunulation.

2. North of this and up to the Scottish border there is a zone with its main axis between Durham and north Lancashire where both lunulation and CC:CP ratios are very variable (2.41–0.15) even for some colonies close together, and much below the 5.0 min. *agestis* figure. (This is generally known as *salmacis*.)

3. Further north *artaxerxes* in south Scotland still shows a moderate degree of lunulation, CC:CP approximately 0.5 which reduces going north until at Inverness lunulation is low, CC:CP approximately 0.15.

4. North of Inverness lunulation is lower still and is considered equal to *allous,* even though white discal spots persist, and we are still dealing with *artaxerxes.*

5. Since *agestis* is the only well-lunulated sub-species, the above indicates penetration as far north as Inverness. This comment is backed up by the presence of dark scales to varying degrees in *artaxerxes* discal spots.

6. On the other hand discal dots, white scales in the discal spots, are found down to the south coast of England (Smyllie *loc. cit.*). They increase somewhat up to the midlands and then significantly in *salmacis* territory.

7. Since *artaxerxes* is the only provider of white discal scales, this indicates some *artaxerxes* penetration right through England.

8. In addition to the interpenetration mentioned in 5–7, an addition of *allous* is also considered necessary to explain some aspects of the data in north England.

9. From all of the above points, we are dealing with a range of hybrids, not distinct species or sub-species.

Lunulation variation during the flight period.

The discovery of univoltine forms at Royston has been noted (Jarvis, 1966) well inside the *agestis* zone. Also, although in cross-breeding experiments the larvae were normally reared in continuous light, details of larval growth under normal conditions were given (Jarvis, 1969) in an experiment where Reading (*agestis*) females were back-crossed with second generation hybrid males via Sherburn (*salmacis*) males and Reading females. The resulting larvae showed variation from *agestis* colouring at one end of the spectrum leading to pupation before the winter, to diapause in more than one instar where the larvae showed increasing *allous* features. There was a variable rate of growth in the brood as a whole, and this would lead to a flight period where individuals with *agestis* characteristics would emerge first to be followed by an increasing trend towards *salmacis*. I had already noted signs of this in the field at Watlington Hill, Oxon (*agestis*), and in 1992 verified that a downward drift in lunulation occurred at Coombs Dale in the Peak District through the flight period. This is a univoltine colony with *agestis* lunulation. Since all colonies show lunulation variation, it seems reasonable to state that they will all show a decrease in lunulation during the flight period, whether in Britain or in Europe. This decrease will be more marked in colonies containing significant percentages of *agestis, artaxerxes* or *allous.*

Mendelism is a theory of heredity tending to reduce to numerical law the recurrence of inherited tendencies. In aspects of the Brown Argus, the possible application of Mendelism has not been overlooked (eg Heslop Harrison and Carter, 1924). I consider that when two Brown Argus adults mate, their resulting progeny will display variation depending on their forebears going back to the time or times when different races were changing their ranges due to climatic or other influences. This can have happened over many years resulting in a complex application of Mendelism, the practical effect being to give a variation in several characteristics, among them upf lunulation. In the case of a typical *agestis* colony the following spectrum will apply for males:–

5 or 6 upf lunules: approximately 4 in 5 (80%). Because of reducing lunulation through the flight period which will have a bearing on what specimens are available to a collector on any particular date, it is not possible to give any meaningful separate figures for 6 and 5. The 0–4 figures are averages, and individuals will be less likely early on and more likely towards the end of any emergence.

4 upfl: approx. 1 in 6	17%
3 upfl: approx. 1 in 50	2%
2 upfl: approx. 1 in 200	0.5%
0 upfl: approx. 1 in 700	0.15%

These figures are not intended to add up precisely to 100%, and arise from an analysis of some 800 males from *agestis* colonies.

The position in north England is much more varied and cannot be expressed so easily. 4–6 upfl will be a maximum of c.90% at the southern end of the zone, eg at Perthichwareu, north Wales, reducing to 25% in parts of Durham. The 4–6 upfl requirement is not stringent, and for females this is 100% for *agestis* colonies and also at Pickering and Perthichwareu where reduction in male lunulation starts. Further north it reduces much more slowly than with males and in a similar "dappled" manner, ie the reduction is not smooth or even.

Table A

When the figures in Table A are compared there is a considerable surprise – the CC:CP ratios for the Swedish sites are below 2.0. It looks as if OH-G's *agestis* equates broadly with *salmacis* in north England. As a preliminary to any comments the differences in generating the data should be understood. Ove Høegh-Guldberg and his co-workers recorded all their dates. The

TABLE A: LUNULATION COMPARISON BETWEEN SWEDEN (S) AND BRITAIN

	Locality	Male C	Male P	Male totals	Female C	Female P	Female total	Combined C	Combined P	Combined total	Ratio of combined totals
1	Sandhammaren (S)	15	47	62	21	14	35	29.5	40.5	70	0.73
2	Skåne less (S)	10	10	20	12	3	15	19.5	10.5	30	1.86
3	S. England	232	49	281	184	11	195	345.0	45.0	390	7.67
4	Surrey	26	10	36	16	-	16	27.6	4.4	32	6.27
5	Peak District	71	16	87	42	-	42	76.3	7.7	84	9.91
6	Perthichwareu	20	28	48	14	-	14	19.8	8.2	28	2.41
7	N. Lancs. OSSD47	23	78	101	22	26	48	32.9	63.1	96	0.52
8	Durham: OSNZ43	10	75	85	39	23	62	46.3	77.7	124	0.60
9	Sherburn Hill	16	13	29	28	11	39	36.8	21.2	58	1.74
10	Hart Warren	2	15	17	2	13	15	3.8	26.2	30	0.15
11	S.W. Scotland	7	28	35	8	7	15	10.3	19.7	30	0.52
12	Perthshire	2	115	117	13	42	55	13.9	96.1	110	0.14
13	Europe: *agestis*	39	11	50	52	1	53	88.1	11.9	100	7.4
14	Europe: *allous*	1	80	81	1	40	41	1.5	80.5	83	0.02

KEY: C = *crassilunulata* P = *parvilunulata*

Smyllie data was generated largely from museum collections and no dates were recorded, only localities. Both methods will give quite satisfactory figures, but OH-G was able to split the Sandhammaren dates into three to provide a first generation *agestis* followed by univoltine *allous* followed by second generation *agestis*. Because the English data is for any one site or area regardless of dates, the Sandhammaren figures have been aggregated for the whole of one year. If they are split up, the best figure, ie the highest CC:CP ratio, works out at 1.38 for the first generation from 24.5 to 18.6. This is of course still very much below the 5.0 minimum. OH-G makes the point that bivoltine *agestis* flies at the same site as univoltine *allous,* and the latter has a larger wing-span than the *agestis.* I suggest that this is similar to Royston, but whereas at Royston the univoltine emergence is a small percentage of the whole, at Sandhammaren it is much larger and comes within the *salmacis* description. In the data for Britain only four *agestis* figures are included, numbers 3-5 and 13 while the *salmacis* sites are numbers 6 to 10. Both south Swedish figures seem to be *salmacis,* but another check can be made from Table B.

Table B

The paragraph on Mendelism above gave the 4–6 upfl percentage for English *agestis* colonies as approximately 97% from data covering 800 or so males. This does not take into account any allowance for chance encounters. Without going into statistics, there is little likelihood of *agestis* colonies having a 4-6 upfl percentage of less than 90%. Surrey (15) at 92% has been included as the lowest *agestis* area for which I have data. Perthichwareu, north Wales also is 92%, but its CC:CP ratio is well below 5.0. This overlap does illustrate the relative lack of focus of the 4–6 upfl percentage which does least well at either end of the lunule spectrum and best in the middle.

TABLE B: COMPARISON OF UPF4-6L% IN BRITAIN, DENMARK, SWEDEN AND NORWAY

LOCALITY			LAT 'N	MALE 4-6 L/T	%	FEMALE 4-6 L/T	%	COMB. %	CLASS'N
1	SSW	Skåne ex Sandh'n	55.3	44/53	83	26/26	100	91.5	2
2	DN	*"agestis"*	56.0	93/122	76	40/40	100	88.0	2
3	SSW	Sandhammaren	55.2	59/121	48	49/54	91	69.5	2
4	SSW	" 2nd Gen.	55.2	18/20	90	12/13	92	91.0	2
5	SW	Gotland	57.5	7/24	29	14/14	100	64.5	2
6	SW	Oland	56.5	9/24	37	6/9	67	52.0	2
7	SNR	Jomfruland	58.8	6/42	14	26/29	90	52.0	2
8	SW	Angermanland	63.5	0/8	0	5/9	56	28.0	3
9	SW	Uppland	60.2	0/19	0	3/8	37	18.5	3
10	NDN	Hirsthals	57.5	5/241	2	25/96	26	14.0	3
11	NNR	Lyngenfjord	69.5	0/9	0	1/5	20	10.0	3
12	ENG	Peak District	53.0	85/87	98	42/42	100	99.0	1
13	ENG	The South *	51.0	214/223	96	137/137	100	98.0	1
14	EUR	*agestis*	–	48/50	96	53/53	100	98.0	1
15	ENG	Surrey	51.3	33/36	92	10/10	100	96.0	1
16	NWA	Perthichwareu	53.2	44/48	92	14/14	100	96.0	2
17	ENG	Sherburn, Durham	54.6	21/29	72	20/20	100	86.0	2
18	ENG	Pickering N. Yorks	54.2	36/44	82	7/7	100	91.0	2
19	ENG	Witherslack	54.3	37/90	41	30/33	91	66.0	2
20	ENG	OSNZ44 Durham	54.8	25/92	27	30/39	77	52.0	2
21	SSC	Solway district	54.9	15/35	43	13/15	87	65.0	2
22	SC	Fifeshire	56.3	5/25	20	14/17	82	51.0	2
23	SC	Aberdeenshire	57.5	8/35	23	23/41	56	39.5	2
24	SC	Perthshire	57.0	16/117	14	34/55	62	38.0	2
25	NSC	N of Inverness	58.0	1/13	8	6/9	67	37.5	2
26	EUR	*allous*	–	7/65	11	14/35	40	25.5	3

NOTES:

1. Sources: 1-11 OH-G, Tables 18 & 19; 12-26 WJS
2. T=total; S=south; N=north; DN=Denmark; NR=Norway; SW=Sweden; EUR=Europe; ENG=England; WA=Wales; SC=Scotland
3. Latitudes are to nearest 0.1' at the localities centre
4. 4-6L/T%s are to nearest whole number, 0.5 rounded down
5. * indicates south of Thames Estuary and the Bristol Channel
6. CLASS'N = classification: 1 *agestis* >95% combined; 2 intermediates 30-95% combined; 3 *allous* <30% combined. Perthichwareu is >95%, but its CC:CP ratio (Table A) is <5, and therefore fails the test for *agestis*
   The border between *allous* and intermediates has been selected at 30% combined. This is an arbitrary figure, but seems reasonably sensible.

However, we have to use the data compiled by OH-G to construct Table B. With male *agestis* figures at over 90%, the combined figures will be 95% minimum. The highest Sandhammaren figure (4 SSW) is for a second generation at 91% combined, and this is equalled by a second generation figure for Denmark. Even these selected figures do not equal the 95% required for *agestis*. There is a genuine difference between English *agestis* and the bivoltine Swedish colonies via two different cross-checks, and the Danish bivoltine colonies show a similar difference in Table B.

Before leaving Table B it is worth commenting on the ssp. *vandalica* colony at Hirsthals. Numbers are high and the values will be stable, well within the *allous* range, and surrounded by colonies with higher lunulation. In Durham significant differences occur between colonies quite close to one another, and in discussing this previously I suggested that towards the end of the climatic optimum after the last ice-age, scrub and woodland had formed. This would restrict the movement of open country non-roaming species like the Brown Argus so that certain areas might be missed from one approach direction and not from another, thus enabling significantly different populations to exist relatively near one another.

Varieties

Var *albiannulata (snelleni)*

In this variety a white ring surrounds the upf discal spot, and examination under a microscope shows clearly that the ring is made up of individual white scales. In England the variety occurs more in females than males, although it can be seen in both. The thickness of the ring can increase with a correspondingly smaller dark central area. On the south coast only one female in ten or so shows the effect and this increases northwards until in Durham/north Lancashire one in three or four is likely. The variety is a stage in the progression from a few white dots (scales) associated with the discal spot to a point where the whole area is covered with scales as far as the naked eye is concerned and the specimen is a "whitespot". This occurs very rarely in *agestis* colonies, and when it does and is noticed it is regarded as quite an event.

OH-G mentions *albiannulata* as occurring fairly frequently in the Jomfruland, south Norway population (in 13 of 71 specimens). The other locality mentioned is Hirsthals, north Denmark where (ssp *vandalica*) it is found "fairly frequently". There is no mention of the form with Danish "*agestis*" or in Sweden. However, in *A Field Guide to the Butterflies of Britain and Europe* (Higgins and Riley, 1970) there is a comment "Rare individuals with white discoidal spot have been recorded from various localities in central and southern England and southern Sweden". In view of this comment I believe examples of var *albiannulata* should occur at least in southern Sweden.

Var *albisignata*

This form occurs regularly in several Scandinavian localities, so is included. It refers to white lines on the uph between the fringe and the dark outer area of the orange lunules, and occurs in most of the populations looked at by OH-G up to Uppland, a little north of Stockholm in Sweden. Further north in Sweden there is not enough data to draw any firm conclusions. A check on 151 British specimens shows that the variety is present in similar levels throughout England and also in Scotland. Again there is a higher percentage in females than in males. The similarities between British and Scandinavian specimens leads to the conclusion that they are part of similar overlaps between sub-species.

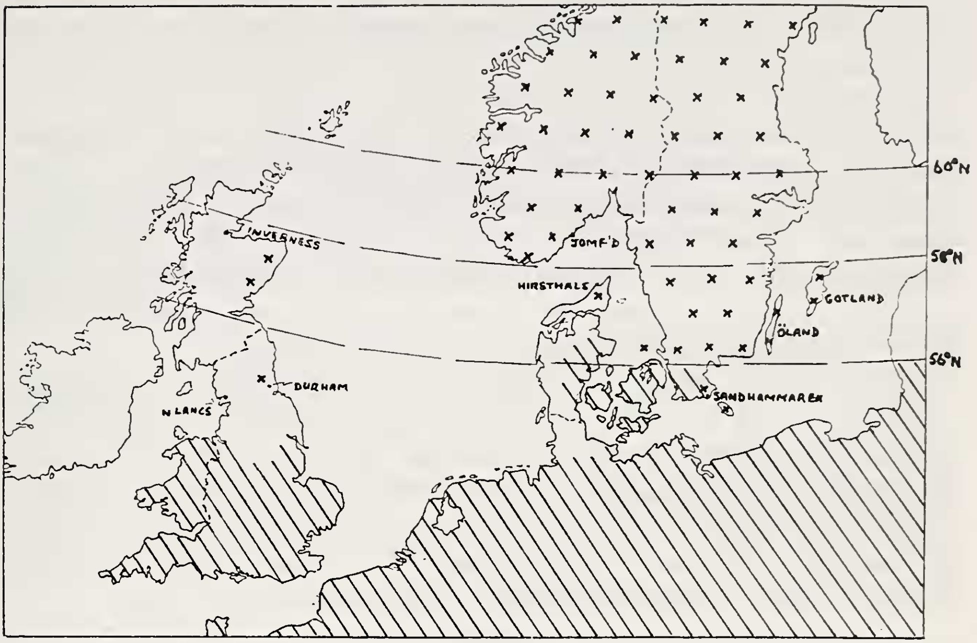
Vars *luxurians* and *unicolor*

There may be alternative words for these forms; *luxurians* refers to specimens with 12 well developed lunules and *unicolor* to those with no lunules on either upper wing. Again both forms are found in Britain and Scandinavia. There does seem to be one significant aspect relating to these varieties: I find it difficult to envisage examples at the opposite ends of the lunulation spectrum without postulating that one of the contributing ancestors must have had no lunules, the other 12. Today the one with no lunules does not seem to be extant. Even at Lyngenfjord there is some lunulation in both males and females. As for 12 lunules *A. cramera* appears to have these but I do not know the species, and the illustrations indicate a different venation. So it may be that again the second ancestor is no longer with us. Put in a different way, subsequent inter-penetration has been great enough to modify the original parents somewhat.

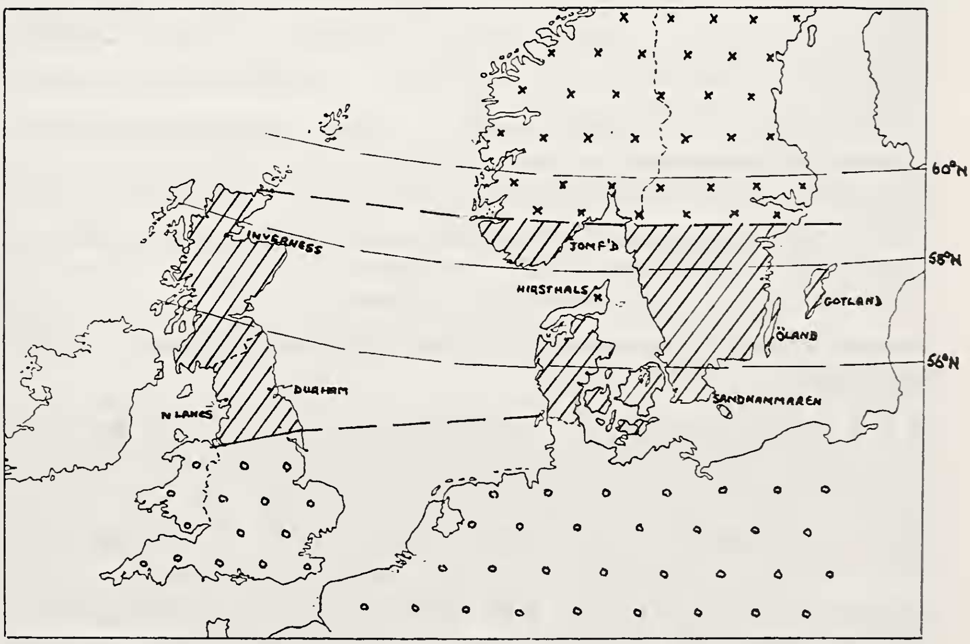
Summary

The main conclusions arise from the comparison of quantified upper forewing lunulation, and the extra focus which this approach has provided has allowed these to be made without taking climate into account. The belief that *agestis* would be bivoltine, and *salmacis* or *allous* univoltine has proved a significant stumbling block to earlier workers.

1. In western Europe, *Ariciae* are represented by *agestis* in the south and *allous* in the north.
2. The boundary between these two sub-species is not clear-cut and is formed by a significant buffer zone (c450km in Scandinavia and 600km in Britain) of intermediate hybrids. For convenience I have used the term *salmacis* in the text to describe the variable race in northern England. I would prefer the term "intermediates" since this is less likely to conjure up any picture of a distinct sub-species.
3. From British data, the boundary between *agestis* and the hybrids is clear-cut, and runs from Perthichwareu in north Wales to Pickering in north Yorkshire.
4. The boundary between *allous* and the hybrids is not clear-cut and has been defined in the present work in a somewhat arbitrary way which roughly coincides with latitude 59°N. In these circumstances Britain only contains *agestis* and the hybrid zone.
5. In this simplified situation *artaxerxes* is considered to be a modification of *allous*.
6. Since the OH-G work stopped at Denmark it is not possible to determine where the change from *agestis* to the hybrids takes place in mainland Europe. This could be in northern Germany.



MAP 1 HØEGH-GULDBERG 1966 agestis allous



MAP 2 SMYLLIE 1994 agestis intermediates allous

One question likely to be asked relates to the possibility of different species being able to retain their individual characteristics after mixing at any one site. Take the case of females which are well lunulated, a "southern" characteristic, and yet are also more likely to have vars *albiannulata* or *albisignata,* both involving extra white scales, a "northern" trend. In aggregate, particularly with lunulation which is easier to count, the figures do give sensible results, but the above variables are jumbled up as far as individuals are concerned. A well lunulated female is perfectly capable of exhibiting *albiannulata* and there is no trend relating these two aspects which are quite random. So there is a tension present which does not equate with the preservation of individual sub-species in their original form.

Maps 1 and 2 compare the conclusions reached by OH-G and Smyllie respectively. OH-G involves *agestis* and *allous,* while Smyllie adds the intermediate zone. Without the very adequate data collected by OH-G and his colleagues this comparison would not have been possible. My hope is that these conclusions represent a few steps forward rather than backward in the road to understanding more about our butterfly fauna. This understanding should help us to be more aware of, and therefore more caring for, our present heritage.

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Broad-bordered Bee hawks in October (*Hemaris fuciformis* L.; Lep.: Sphingidae)

Mr Ron Hoblyn witnessed two of these moths feeding at *Nicotiana* flowers in his garden at Santon Dowham, Suffolk, on 4th October 1994. The species has long been known to frequent the rides and open spaces of Thetford Forest and adjoining breckland, where in June and July it could be seen at Viper's Bugloss blossom. In recent years moths have appeared at garden flowers in locations well away from the forest, and larvae and eggs in the forest on honeysuckle in sunny situations as well as in shady woodland. Whatever its national status may be, this species continues to do well here and has enjoyed some very good seasons.– G.M. HAGGETT, Meadows End, Northacre, Caston, Norfolk.